

Use of Shallow Lagoon Habitats by Nekton of the Northeastern Gulf of Mexico

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Abstract We compared nekton use of prominent habitat types within a lagoonal system of the northeastern Gulf of Mexico (GoM). These habitat types were defined by combinations of structure (cover type) and location (distance from shore) as: *Spartina* edge (≤ 1 m from shore), *Spartina* (3 m from shore); *Juncus* edge (≤ 1 m from shore); seagrass located 3, 5, and 20 m from shore; and shallow non-vegetated bottom at various distances from shore. Although seagrass and *Spartina* edge sites differed little in environmental characteristics, the density and biomass of most abundant taxa, including pink shrimp (*Farfantepenaeus duorarum*), were higher in seagrass. Most species within seagrass and *Spartina* did not differ in abundance or biomass with distance from shore. Our study revealed a shift in peak habitat use in the northeastern GoM to seagrass beds from the pattern observed to the west where nekton is concentrated within shoreline emergent vegetation.

Keywords Seagrass · Salt marsh · Habitat comparison · Pink shrimp · *Farfantepenaeus duorarum* · Florida lagoon

Introduction

Estuaries in the Gulf of Mexico (GoM) vary widely in climate, size, geomorphology, freshwater inflow, and wetland coverage; all of these characteristics may influence nekton (fishes and natant crustaceans) distribution (Deegan et al. 1986; Turner 2001). North of Naples, Florida, in the east and Cape Rojo, Mexico, in the west, the climate along the northern GoM is classified as warm temperate and to the south as tropical (Briggs 1974). The Mississippi and Atchafalaya rivers in Louisiana dominate this region's freshwater supply, and river-dominated estuaries are prominent features of the coast here. Freshwater inflow to estuaries decreases dramatically to the east and west of Louisiana. In non-river-dominated systems, where riverine input rarely exceeds $500 \text{ m}^3 \text{ s}^{-1}$, freshwater supply is a product of local watersheds and coastal rainfall (Solis and Powell 1999).

The mix and areal coverage of aquatic habitats within GoM estuaries also varies in concert with changes in climate, river inflow, and intertidal area (Deegan et al. 1986; Turner 2001). The vast coastal marshes centered in southeast Louisiana gradually give way east and west to barrier island chains that partially enclose shallow sounds and lagoons. Seagrass beds dominated principally by turtle grass (*Thalassia testudinum*), shoal grass (*Halodule wrightii*), manatee grass (*Syringodium filiforme*), and star grass (*Halophila engelmannii*) occur most extensively east of Mobile Bay, Alabama, and west of Galveston Bay, Texas, where salinity and water clarity are relatively high (Handley et al. 2007; Merino et al. 2009). The river-dominated estuaries of Louisiana generally lack seagrasses.

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Nekton density patterns have been documented and compared for a variety of shallow estuarine habitats in the northern GoM (see reviews by Minello 1999; Heck et al. 2003; Minello et al. 2003; Sheridan and Hays 2003). Salt marsh and seagrass beds, in particular, are widely recognized as essential habitat for fishery species based mainly on an examination of these nekton density patterns. Few studies, however, have directly compared nekton densities in seagrass and marsh together, and the body of literature from this work is geographically biased as no comparison has been done in estuaries east of Mobile Bay (Minello et al. 2003; Dantin et al. 2005). Thomas et al. (1990) and Heck et al. (2001) compared blue crab (*Callinectes sapidus*) densities among emergent marsh, seagrass, and shallow non-vegetated bottom (SNB) in estuaries of Texas and Alabama, respectively. Stunz et al. (2002) compared the densities of recently settled red drum (*Sciaenops ocellatus*) in these habitat types in Galveston Bay, TX. The densities of all abundant nekton were compared among these habitat types from a south Texas estuary (Rozas and Minello 1998). Additional research on this topic is warranted, especially studies from the northeastern GoM. Such studies would provide much needed information on the relative habitat value of seagrass and salt marsh and may reveal important linkages between these essential habitat types (Raposa and Oviatt 2000; Dantin et al. 2005).

Direct comparisons of nekton densities among habitats that employ the same quantitative sampling gear provide a good measure of habitat value and represent an initial step in identifying essential fish habitat (Minello 1999; Beck et al. 2001). Information derived from these studies can be used to determine the role of habitats in supporting coastal fisheries and to develop sound management plans for estuaries and species that depend on coastal habitats.

Our objective was to examine the distribution of nekton among the major habitat types of the St. Andrew Sound system, a northeastern GoM estuary. A goal of our study was to determine whether assumptions about nekton distributions among habitat types developed from the north-central and northwestern GoM could be extended to the northeast. Densities and biomasses of fishery species and other nekton were measured and compared among seagrass beds, emergent marsh vegetation, and SNB. By sampling at different distances from the shoreline, we examined whether distance from adjacent habitat types affected nekton distributions. We also compared flooding patterns among habitat types in this seagrass-dominated system.

Materials and Methods

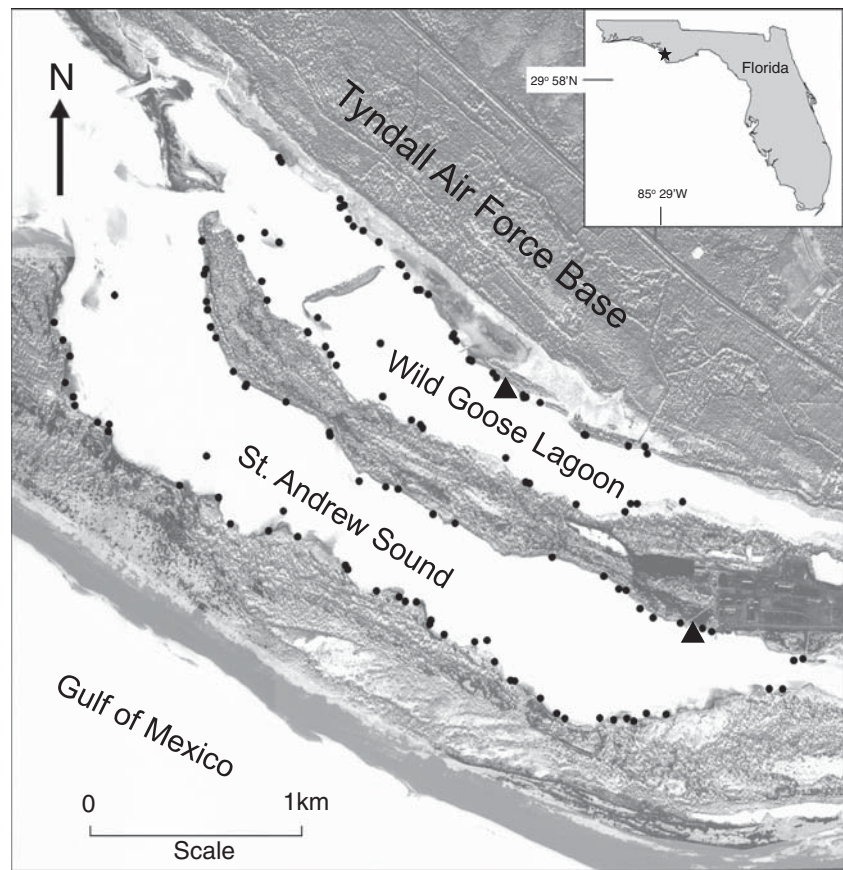
St. Andrew Sound is a coastal lagoon, approximately 16 km long by 1.6 km wide (area=1,905 ha), located in the Florida

panhandle (Fig. 1). Salinity ranges from 25 to 36, and the mean range of tide at the nearby NOAA tide gauge (no. 8729210) is 0.37 m. A single inlet created in 1975 by Hurricane Eloise connects the sound with the GoM. Seagrass coverage within the sound has remained stable at 336–370 ha since 1940 primarily because the shoreline around the sound, which is managed by Tyndall Air Force Base, has remained relatively unaltered (Handley et al. 2007). Our study focused on the extensive seagrass beds, tidal marshes, and SNB located southeast of the lagoon inlet within Wild Goose Lagoon and St. Andrew Sound (Fig. 1). Seagrass beds consisted mainly of turtle grass, but also contained shoal grass. Marsh vegetation in the intertidal zone was dominated by *Juncus roemerianus* or *Spartina alterniflora*.

Our study was designed to examine the distribution of nekton within the lagoonal system as a measure of habitat quality by sampling seven different habitat types defined by cover type and location (distance from shore): (1) *S. alterniflora* marsh ≤ 1 m from shore (*Spartina* edge), (2) *S. alterniflora* marsh 3 m from shore (*Spartina* 3 m), (3) *J. roemerianus* marsh ≤ 1 m from shore (*Juncus* edge), (4) seagrass 1 m from shore (seagrass 1 m), (5) seagrass 5 m from shore (seagrass 5 m), (6) seagrass 20 m from shore (seagrass 20 m), and (7) SNB located at various distances from shore. We collected nine replicate samples during daylight and at high tide from each habitat type during spring (May 31–June 1) and fall (September 19–20) 2006 for a total of 126 samples. Sample sites within habitat types were randomly selected using random numbers and a grid placed over an aerial photograph. Two boats and crews of three persons each simultaneously collected these samples over two consecutive days during each sampling event.

We quantitatively sampled nekton using 1-m² drop samplers and the method described by Zimmerman et al. (1984). We selected this gear because it is effective in capturing shallow-burrowing animals such as pink shrimp (*Farfantepenaeus duorarum*) that we targeted in our study and similarly efficient in all the habitat types we sampled (Sheridan et al. 1997; Rozas and Minello 1997). Pink shrimp may avoid towed gear (e.g., trawls, seines, crab scrapes) by burrowing during the day (Greening and Livingston 1982). Immediately after the drop sampler enclosed an area, we measured water temperature and dissolved oxygen using a handheld meter. Water depth was determined by averaging five depth measurements taken within the sampler. We measured the distance from the center of the sampler to the nearest marsh shoreline and to the nearest edge of the seagrass bed using a meter tape or laser range finder. We also collected a water sample from which turbidity and salinity were determined later in the laboratory. Turbidity was measured using a nephelometer and a formazin standard, and salinity was determined with a temperature-compensated refractometer.

Fig. 1 Map showing the study area (St. Andrew Sound and Wild Goose Lagoon) and its location on the Florida coast. Locations of nekton sample sites (solid circles) and two temporary tide gauges (solid triangles) also are shown



Plant stems at marsh sites were clipped at the substrate, counted, and removed from the sampler. At seagrass sites, we estimated coverage (0–100%) and identified the plant species present. Aboveground seagrass shoots were clipped, vigorously shaken to detach any animals possibly contained in the vegetation, and removed from the sampler.

After measuring the environmental variables and removing vegetation, we removed the animals using dip nets and filtering the water pumped out of the sampler through a 1-mm mesh net. When the sampler was completely drained, we removed by hand any animals remaining in the sampler. Samples were preserved in formalin and returned to the laboratory for processing.

In the laboratory, animals were removed from each sample and identified to the lowest feasible taxon. We used the nomenclature of Perez-Farfante and Kensley (1997) for penaeid shrimps and identified individuals <18 mm total length (TL) to species using the methods described by Alvarado Bremer et al. (2010) and Ditty and Alvarado Bremer (2011). Shrimps >35 mm TL were identified to species using the protocol described in Rozas and Minello (1998). Even so, 281 specimens of *Farfantepenaeus* could not be reliably identified either because of their size (257 individuals 18–35 mm TL) or because they were damaged (24 individuals) and lacked body parts necessary for identification. These unidentified *Farfantepenaeus* (42%

and 35% of total in spring and fall, respectively), grass shrimps *Palaemonetes* spp. (38% and 27% of total in spring and fall, respectively), and swimming crabs *Callinectes* spp. (25% and 32% of total in spring and fall, respectively) were classified based on the proportion of identified species in each sample (Rozas and Minello 1998). Individuals of a species in each sample were pooled to determine biomass (wet weight) to the nearest 0.1 g.

We used the density and biomass data for pink shrimp and blue crab to compare standing crops among selected habitats (seagrass, *Spartina* edge, *Juncus* edge, SNB). The areal coverage of seagrass and SNB was calculated using GIS and a recent aerial photograph of the study area. A handheld GPS was used in the field to estimate length of shoreline occupied by *Spartina* edge and *Juncus* edge. Intertidal marsh >1 m from shore was excluded from these estimations of aerial coverage because *Spartina* 3 m was difficult to delineate and because other than this habitat type no nekton samples were collected in marsh vegetation beyond 1 m from shore. Standing crops of pink shrimp and blue crab were estimated for spring and fall by multiplying the average animal density and biomass determined from nekton samples collected each season by the total area of each habitat type within the study area. Standing crops for seagrass were computed by multiplying the total area of seagrass in the study area by the mean of all ($n=27$) density

or biomass samples collected within seagrass (1, 5, and 20 m) each season.

The EPA Gulf Ecology Division provided water level data collected from temporary tide gauges established May 12, 2005 to October 22, 2006 in St. Andrew Sound and Wild Goose Lagoon (Fig. 1). The data from these two temporary gauges were regressed against water level data collected over the same time period at Panama City Beach, FL (NOAA Station ID 8729210) to derive equations that can be used to predict water levels in the sound and lagoon from the historical NOAA tide gauge data. We estimated the flooding durations of our nekton sample sites by relating the water depth measured at each sample site to concurrent tide data in the appropriate water body (St. Andrew Sound or Wild Goose Lagoon) calculated from these derived equations.

Data Analyses

We used one-way analysis of variance (ANOVA) to compare the densities of individual species among the habitat types followed by a priori contrasts (JMP, version 8.0.2, SAS Institute, Inc., Cary, NC, 2009). Comparable analyses also were conducted for nekton biomass, species richness, and environmental variables. Contrasts were designed to make the following comparisons: *Spartina* edge vs. seagrass (all distances combined), *Spartina* edge vs. SNB, *Spartina* edge vs. *Spartina* 3 m, *Spartina* edge vs. *Juncus* edge, seagrass 1 m vs. seagrass 5 m, and seagrass 1 m vs. seagrass 20 m. The first four comparisons contrasted means in *Spartina* edge and the other habitat types we sampled. The last two comparisons tested for differences in means within seagrass beds among sites located at three distances from the marsh.

In the ANOVA procedure, we analyzed the data separately for each season because several species were only abundant enough to include in the statistical analysis in one season. We considered alpha levels of 0.05 to be statistically significant in all results, but we also assessed significance after adjusting alpha levels for the habitat type effect using the sequential Bonferroni method described by Rice (1989), which buffers against error introduced by making multiple comparisons with the same sample set (i. e., testing a hypothesis for several species or variables). Mean densities and biomasses were positively related to the standard deviation, so we used $\ln(x+1)$ transformations on the original values prior to analyses. Environmental variables and species richness were not transformed. All tabular and graphical data presented in this paper are untransformed means.

We also used regression trees to further explore potential relationships between the distribution of juvenile pink

shrimp and environmental characteristics. Univariate analyses were performed using recursive partitioning available in the JMP software. Trees are constructed from a series of mutually exclusive binary splits. The splitting approach minimizes the within-group sum of squares (SS) while maximizing the between-groups SS for each level in the tree (Deáth 2002). The relative importance of each explanatory variable in the tree decreases with each split; the first split accounts for most of the overall variance in the model, and subsequent splits explain increasingly less. Each model included the response variable of shrimp density, a single categorical explanatory variable (habitat type), and seven continuous explanatory variables (salinity, water temperature, DO, water depth, turbidity, distance to marsh edge, distance to seagrass edge). We analyzed the data collected in spring and fall separately to look for possible seasonal differences in the response of shrimp to environmental conditions. The JMP software allows users to select the number of splits used in the model. Therefore, we increased the number until adding another split would explain <5% more of the overall variation in the model (i.e., increase $R^2 < 0.05$). We used the k -fold cross-validation ($k=5$) in JMP to compute a cross-validated overall R^2 for each model.

Results

We collected totals of 4,933 individuals, 25 species, and 0.8 kg total biomass of crustaceans and 1,185 individuals, 29 species, and 1.3 kg total biomass of fishes during our study (Table 1). The most abundant crustaceans included brackish grass shrimp (*Palaemonetes intermedius*), pink shrimp, zostera shrimp (*Hippolyte zostericola*), bigclaw snapping shrimp (*Alpheus heterochaelis*), daggerblade grass shrimp (*Palaemonetes pugio*), and blue crab (Tables 1 and 2). Blue crab, thinstripe hermit crab (*Clibanarius vittatus*), bigclaw snapping shrimp, Atlantic mud crab (*Panopeus herbstii*), pink shrimp, and brackish grass shrimp contributed most to total crustacean biomass (Appendix 1). Pinfish (*Lagodon rhomboides*), rainwater killifish (*Lucania parva*), and darter goby (*Ctenogobius boleosoma*) were the most abundant fishes identified from our samples (Tables 1 and 2). Most of the fish biomass in our samples was from pinfish, American eel (*Anguilla rostrata*, one individual), white mullet (*Mugil curema*), spot (*Leiostomus xanthurus*), and rainwater killifish (Appendix 1).

Densities of the most abundant taxa were concentrated in emergent vegetation and seagrass beds, but patterns of distribution among habitat types were not always consistent among taxa or even within a taxon between spring and fall (Table 2). Densities of total crustaceans (spring), total fishes (spring), and the most abundant taxa were higher in

Table 1 List of species collected with mean densities over two seasons in aggregated habitat type

Species	Common name	Mean density (number per square meter)		
		Seagrass	Marsh	SNB
Crustaceans				
<i>Palaemonetes intermedius</i>	Brackish grass shrimp	7.33	10.22	0.22
<i>Farfantepenaeus duorarum</i>	Pink shrimp	11.78	1.54	2.72
<i>Hippolyte zostericola</i> ^a	Zostera shrimp	10.20	0.06	0.00
<i>Palaemonetes pugio</i>	Daggerblade grass shrimp	5.81	3.57	0.06
<i>Alpheus heterochaelis</i>	Bigclaw snapping shrimp	6.02	2.72	0.72
<i>Callinectes sapidus</i>	Blue crab	2.35	2.06	0.89
<i>Clibanarius vittatus</i>	Thinstripe hermit crab	1.07	2.15	0.22
<i>Palaemonetes vulgaris</i>	Marsh grass shrimp	0.63	1.76	0.00
<i>Dsypanopeus texana</i>	Gulf grassflat crab	1.17	0.35	0.06
<i>Sesarma reticulatum</i> ^a	Purple marsh crab	0.00	0.33	0.00
<i>Armases cinereum</i> ^a	Squareback marsh crab	0.00	0.33	0.00
<i>Farfantepenaeus aztecus</i>	Brown shrimp	0.17	0.13	0.06
<i>Callinectes similis</i> ^a	lesser blue crab	0.11	0.11	0.06
<i>Eurypanopeus depressus</i>	flatback mud crab	0.13	0.07	0.11
<i>Macrobrachium ohione</i> ^a	Ohio shrimp	0.17	0.00	0.00
<i>Panopeus turgidus</i>	Ridgeback mud crab	0.15	0.00	0.06
<i>Alpheus normanni</i> ^a	Green snapping shrimp	0.06	0.09	0.00
<i>Ambidexter symmetricus</i> ^a	Night shrimp	0.13	0.00	0.00
<i>Tozeuma cornutum</i> ^a	Gorgonian toothpick shrimp	0.06	0.00	0.00
<i>Eurytium limosum</i> ^a	Broadback mud crab	0.02	0.02	0.00
<i>Uca pugnax</i> ^a	Atlantic marsh fiddler	0.00	0.04	0.00
<i>Libinia dubia</i> ^b	Longnose spider crab	0.02	0.00	0.00
<i>Limulus polyphemus</i> ^b	Horseshoe crab	0.00	0.02	0.00
<i>Microphrys bicornutus</i> ^a	Speck-claw Decorator crab	0.00	0.02	0.00
<i>Stenocionops furcatus</i> ^b	Furcate spider crab	0.02	0.00	0.00
Fishes				
<i>Lagodon rhomboides</i>	Pinfish	2.78	3.02	0.11
<i>Lucania parva</i>	Rainwater killifish	3.39	2.07	0.11
<i>Ctenogobius boleosoma</i>	Darter goby	2.65	1.28	0.33
<i>Eucinostomus argenteus</i>	Spotfin mojarra	0.65	0.20	0.44
<i>Myrophis punctatus</i>	Speckled worm eel	0.52	0.17	0.00
<i>Syngnathus scovelli</i>	Gulf pipefish	0.37	0.22	0.11
<i>Leiostomus xanthurus</i>	Spot	0.06	0.43	0.22
<i>Gobiosoma robustum</i> ^a	Code goby	0.20	0.22	0.39
<i>Lutjanus griseus</i>	Gray snapper	0.33	0.15	0.11
<i>Poecilia latipinna</i>	Sailfin molly	0.09	0.39	0.00
<i>Bairdiella chrysoura</i>	Silver perch	0.33	0.00	0.00
<i>Cyprinodon variegatus</i>	Sheepshead minnow	0.11	0.19	0.00
<i>Mugil curema</i> ^a	White mullet	0.04	0.11	0.33
<i>Gobiosoma longipala</i> ^a	Twoscale goby	0.06	0.00	0.44
<i>Gobiosoma bosc</i> ^a	Naked goby	0.00	0.11	0.11
<i>Lucania goodei</i> ^a	Bluefin killifish	0.00	0.15	0.00
<i>Symphurus plagiusa</i> ^a	Blackcheek tonguefish	0.04	0.00	0.22
<i>Opsanus beta</i> ^a	Gulf toadfish	0.06	0.02	0.06
<i>Sciaenops ocellatus</i> ^a	Red drum	0.00	0.06	0.00
<i>Adinia xenica</i> ^a	Diamond killifish	0.00	0.04	0.00

Table 1 (continued)

Species	Common name	Mean density (number per square meter)		
		Seagrass	Marsh	SNB
<i>Fundulus similis</i>	Longnose killifish	0.00	0.04	0.00
<i>Syngnathus louisianae</i> ^a	Chain pipefish	0.04	0.00	0.00
<i>Anguilla rostrata</i> ^a	American eel	0.00	0.02	0.00
<i>Achirus lineatus</i> ^a	Lined sole	0.02	0.00	0.00
<i>Gobionellus oceanicus</i> ^a	Highfin goby	0.02	0.00	0.00
<i>Hyporhamphus meeki</i> ^a	False silverstripe Halfbeak	0.02	0.00	0.00
<i>Lutjanus synagris</i> ^a	Lane snapper	0.02	0.00	0.00
<i>Microgobius gulosus</i> ^a	Clown goby	0.02	0.00	0.00
<i>Orthopristis chrysoptera</i> ^a	Pigfish	0.02	0.00	0.00

Mean densities were estimated from 54 seagrass, 54 marsh, and 18 SNB samples

Seagrass seagrass 1, 5, and 20 m from shore; Marsh *Spartina* edge, *Juncus* edge, and *Spartina* 3 m from shore; SNB shallow nonvegetated bottom

^a Collected only in fall

^b Collected only in spring

seagrass than *Spartina* edge. The highest densities of juvenile pink shrimp occurred in seagrass beds in both spring and fall (Table 2 and Fig. 2). Within seagrass, the densities of these young shrimps in spring were higher at sites 20 m from shore than at sites near the marsh, but in fall, shrimps were evenly distributed within the seagrass (Table 2). Darter goby in fall was more abundant within seagrass beds near (1 m) than 20 m from shore. Daggerblade grass shrimp (spring), rainwater killifish (spring), and bigclaw snapping shrimp (fall) were all more abundant in seagrass beds than *Spartina* edge. We also collected more species at seagrass than *Spartina* edge sites in spring, but in fall, no significant difference was detected in species richness between these two habitat types.

No species had significantly higher densities in *Spartina* edge than seagrass beds (Table 2). Some species, however, had relatively high densities within emergent marsh vegetation, and nekton densities in marshedge were generally higher than over SNB. Within *Spartina* marsh, the densities of brackish grass shrimp and darter goby in fall were higher at the marsh edge than in *Spartina* 3 m. Total crustaceans (spring) and pinfish (fall) densities were higher in *Juncus* edge than *Spartina* edge. In fall, total fishes, total crustaceans, brackish grass shrimp, darter goby, and rainwater killifish densities were higher in *Spartina* edge than over SNB (Table 2).

Few differences in biomass among habitat types were detected, and all statistically significant habitat contrasts occurred in the fall data (Appendix 1). We collected more brackish grass shrimp biomass at *Spartina* edge than at seagrass, *Spartina* 3 m, or SNB sites. The mean biomass for bigclaw snapping shrimp was greater at seagrass than

Spartina edge sites. The mean biomass of total fishes, pinfish, and thinstripe hermit crabs was greater in *Juncus* edge than *Spartina* edge. Rainwater killifish had more biomass in *Spartina* edge than SNB sites.

Standing crops of pink shrimp and blue crab were higher in seagrass beds than in any other habitat type because seagrass beds contained relatively high densities of these species and occupied a large portion (47%) of the study area (Table 3). The area of marsh habitat used by these species was likely underestimated (marsh >1 m from shore was excluded), but this discrepancy is relatively unimportant because of the low densities in marsh habitats. If we assumed a 10-m-wide band of marsh around the study lagoon with pink shrimp densities in the *Juncus* marsh equal to that in *Juncus* edge and densities in the *Spartina* marsh equal to the mean of *Spartina* edge and *Spartina* 3 m marsh, seagrass still would support approximately 210 and 76 times more pink shrimp than marsh in spring and fall, respectively. Similarly, seagrass would support about 15 and 11 times more blue crab in spring and fall, respectively than a 10-m band of marsh.

The differences in environmental variables among habitat types were consistent between spring and fall (Appendix 2). Water depth within the water bodies increased with distance from the marsh. Within *Spartina* marsh, water depth decreased with distance from shore. Water temperature, salinity, dissolved oxygen concentration, and turbidity levels were all similar among habitat types. Seagrass cover was high (89–100%), and no difference in cover was detected among the three seagrass habitat types. Stem density was significantly higher at *Juncus* edge than *Spartina* edge sites and in fall was higher at *Spartina* 3 m than *Spartina* edge sites.

Table 2 Mean densities as numbers per square meter (SE) of abundant decapod crustaceans and fishes collected among seven habitat types including three types of marsh (*Spartina* edge and *Juncus* edge ≤ 1 m from shore, *Spartina* 3 m from shore); three types of seagrass (seagrass 1, 5, and 20 m from shore); and SNB in May–June and September 2006

Species	<i>Spartina</i> 3 m		<i>Spartina</i> edge		<i>Juncus</i> edge		Seagrass 1 m		Seagrass 5 m		Seagrass 20 m		SNB		Total number collected	Habitat effect <i>p</i> value	Contrast <i>p</i> values					
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	(1) <i>Spartina</i> edge vs. seagrass	(2) <i>Spartina</i> edge vs. SNB			(3) <i>Spartina</i> edge vs. <i>Spartina</i> 3 m edge	(4) <i>Spartina</i> edge vs. <i>Juncus</i> edge	(5) Seagrass 1 m vs. 5 m	(6) Seagrass 20 m vs. 5 m		
May–June 2006																						
Crustaceans	45.7	(38.68)	3.8	(1.67)	8.9	(2.02)	8.2	(2.69)	43.0	(23.22)	13.7	(3.10)	1.8	(0.78)	1315	0.0026 ^a	0.0041	0.5783	0.0582	0.0480	0.0469	0.2468
Daggerblade grass shrimp	14.4	(11.67)	0.1	(0.11)	3.0	(1.18)	2.0	(1.18)	22.2	(18.04)	4.4	(1.49)	0.0	(0.00)	416	0.0308	0.0120	0.8844	0.0802	0.0996	0.0974	0.2768
Brackish grass shrimp	18.8	(17.43)	0.4	(0.44)	1.2	(0.57)	1.0	(0.60)	4.9	(4.40)	1.4	(0.88)	0.2	(0.22)	252	0.6209						
Pink shrimp	0.1	(0.11)	0.3	(0.24)	0.3	(0.24)	1.2	(0.57)	8.2	(4.59)	8.2	(2.75)	1.4	(0.50)	179	0.0001 ^a	0.0019	0.1462	0.7458	1.0000	0.0560	0.0024
Marsh grass shrimp	9.8	(9.05)	0.0	(0.00)	0.6	(0.56)	0.9	(0.89)	1.0	(1.00)	0.9	(0.77)	0.0	(0.00)	118	0.5557						
Blue crab	0.2	(0.15)	0.2	(0.15)	2.2	(0.97)	1.2	(0.78)	5.7	(3.13)	0.4	(0.24)	1.3	(0.75)	102	0.0983						
Fishes	9.7	(7.21)	3.3	(1.09)	6.3	(2.40)	12.9	(4.54)	8.9	(3.94)	13.8	(4.33)	0.9	(0.77)	502	0.0037 ^a	0.0328	0.0941	0.7180	0.5249	0.2604	0.7773
Pinfish	8.7	(7.08)	1.2	(0.46)	3.7	(1.82)	2.8	(1.19)	1.4	(0.77)	6.8	(2.43)	0.2	(0.15)	223	0.0499	0.2523	0.2673	0.3509	0.3418	0.5131	0.0970
Rainwater killifish	0.1	(0.11)	0.2	(0.22)	0.0	(0.00)	6.0	(2.99)	2.4	(1.07)	5.4	(3.20)	0.2	(0.22)	130	0.0060 ^a	0.0072	1.0000	0.9076	0.7531	0.3798	0.5228
Species Richness	3.6	(0.53)	3.3	(0.83)	5.1	(0.75)	5.3	(0.99)	6.4	(1.42)	6.6	(0.77)	2.0	(0.75)	28	0.0043 ^a	0.0098	0.2989	0.8619	0.1676	0.3860	0.3406
September 2006																						
Crustaceans	79.3	(45.43)	52.4	(33.55)	26.6	(2.46)	40.1	(18.09)	84.8	(56.39)	48.2	(15.18)	4.4	(2.31)	3,618	0.0423	0.5737	0.0199	0.8503	0.4931	0.7678	0.7612
Brackish grass shrimp	1.1	(0.70)	29.6	(19.07)	10.2	(2.47)	10.9	(6.96)	14.6	(5.33)	11.2	(5.68)	0.2	(0.15)	700	0.0047 ^a	0.3040	0.0021	0.0082	0.9651	0.2487	0.9414
Pink shrimp	1.4	(0.63)	4.6	(1.75)	2.4	(0.60)	18.2	(5.21)	17.0	(3.92)	17.8	(6.43)	4.0	(2.07)	589	0.0015 ^a	0.0108	0.7241	0.2897	0.7241	0.4729	0.9655
Zostera shrimp	0.0	(0.00)	0.3	(0.33)	0.0	(0.00)	10.3	(10.21)	37.7	(34.73)	13.2	(6.70)	0.0	(0.00)	554	0.0578						
Bigclaw snapping shrimp	0.0	(0.00)	9.3	(8.96)	7.0	(2.24)	10.4	(4.56)	12.1	(6.93)	10.0	(5.22)	1.3	(0.90)	452	0.0130	0.0461	0.7118	0.2677	0.0929	0.5968	0.5096
Blue crab	4.6	(2.33)	3.3	(1.91)	1.8	(1.19)	3.4	(1.77)	2.8	(1.53)	0.6	(0.44)	0.4	(0.24)	152	0.2562						
<i>Macrobrachium</i> spp.	0.0	(0.00)	0.4	(0.44)	0.2	(0.22)	0.4	(0.44)	13.1	(13.11)	1.9	(1.89)	0.1	(0.11)	146	0.8330						
Fishes	5.4	(1.21)	15.8	(3.13)	13.1	(2.43)	11.2	(3.18)	16.9	(4.57)	8.9	(2.75)	5.1	(1.93)	683	0.0220	0.3586	0.0089	0.0510	0.9748	0.3197	0.3273
Darter goby	0.6	(0.29)	5.4	(2.22)	1.7	(0.87)	5.6	(2.06)	5.3	(2.55)	1.1	(0.70)	0.7	(0.24)	183	0.0165	0.4470	0.0350	0.0184	0.1237	0.4511	0.0113
Rainwater killifish	2.2	(0.91)	6.9	(3.75)	3.0	(1.46)	1.8	(1.00)	4.6	(2.35)	0.1	(0.11)	0.0	(0.00)	167	0.0084	0.0841	0.0031	0.3746	0.4687	0.1581	0.1435
Pinfish	0.1	(0.11)	0.4	(0.34)	4.0	(1.89)	1.0	(0.37)	1.2	(0.49)	3.4	(1.94)	0.0	(0.00)	92	0.0058	0.1073	0.4765	0.6346	0.0050	0.8609	0.4025
Species Richness	5.8	(0.83)	7.0	(1.52)	8.8	(0.36)	9.1	(1.32)	10.0	(1.19)	7.4	(1.65)	4.8	(1.39)	54	0.0516						

The mean number of species (fishes and crustaceans) collected per sample in each habitat type is presented as species richness. Means were estimated from nine samples in each habitat type. The results (*p* values) are given from ANOVAs used to compare all habitat types (habitat effect) and six a priori contrasts testing different habitat combinations. Degrees of freedom = 6,56 for the ANOVA test of habitat

^aThe ANOVA probability value was significant at the 5% level after alpha was adjusted as described by Rice (1989). Contrast *p* values were not adjusted

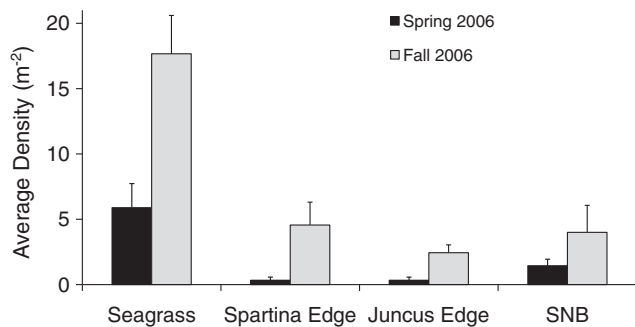


Fig. 2 Distribution of pink shrimp among habitat types in May–June and September 2006. Means are estimated from 27 seagrass samples and nine samples for each of the other habitat types. Error bars, 1 SE

The results of the recursive partitioning analyses were consistent with the ANOVA results. Habitat type was the most important variable explaining pink shrimp distribution in each model (Figs. 3 and 4). In spring, pink shrimp was more abundant in seagrass beds located 5 and 20 m from shore than in the other habitat types, and the selected model explained 26% of the variation in the data using the single predictor, habitat type (Fig. 3). The second model explained 62% of the variation in pink shrimp distribution in fall. In this model, water depth formed a secondary split on the primary split of habitat type, which included the combined seagrass types. Pink shrimp densities in fall were higher in seagrass beds than in other habitat types, and within seagrass, densities were higher at depths <66 cm (Fig. 4).

Flooding durations varied among habitat types, and as expected, seagrass and SNB sites flooded for longer periods each month than marsh sites (Fig. 5). Mean monthly flooding durations by habitat type for 2006 were: SNB=97%, seagrass 20 m=98%, seagrass 5 m=95%, seagrass 1 m=92%, *Spartina* edge=84%, *Juncus* edge=78%, and *Spartina* 3 m=74%. Water levels also varied seasonally, and the highest levels during the year occurred in April–October (Fig. 5). Seagrass and SNB sites were inundated almost continuously ($\geq 95\%$) during these 7 months. *Spar-*

tina edge sites were inundated >85% of the time, April–October, and these sites flooded for longer periods each month than either *Juncus* edge or *Spartina* 3 m sites.

Discussion

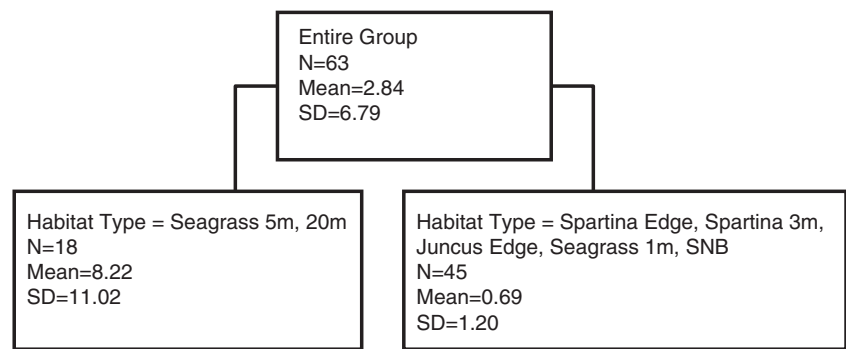
Seagrass provided important habitat support for fishes and crustaceans in the seagrass-dominated lagoonal system of our study area. Young pink shrimps, for example, were 19.6 and 3.8 times more abundant in seagrass than *Spartina* edge in spring and fall, respectively. Regression trees also revealed the highest densities of pink shrimp in seagrass; in fall, the mean densities were 17.7 m^{-2} in seagrass vs. 3.1 m^{-2} in other habitat types. Seagrass beds also supported most of the pink shrimp standing crop (80% of individuals and 98% of the biomass) in fall when this species was most abundant in the study area. Pink shrimp was the dominant penaeid species in our samples (<1% of specimens were identified as brown shrimp, *Farfantepenaeus aztecus*), but distinguishing the young of these two species is still challenging (Alvarado Bremer et al. 2010; Ditty and Alvarado Bremer 2011). Pink shrimps account for most of the larger penaeid shrimps taken in St. Andrew Bay, which is located just north of our study area (Brusher and Ogren 1976), and this species may compose up to 97% of the abundance and 99% of the biomass of penaeid shrimps in some tropical seagrass-dominated lagoons (Sánchez 1997). Our mean pink shrimp densities within seagrass beds of 6–18 shrimps per square meter are comparable to the densities in seagrass reported from other locations in Florida (Holmquist et al. 1989; Sheridan 1992; Sheridan et al. 1997; Matheson et al. 1999; Glancy et al. 2003) and south Texas (Sheridan and Minello 2003). Decades ago, Hoese and Jones (1963) recognized the potential importance of seagrass beds along the northern GoM as inshore nursery areas for pink shrimp. This species is a dominant decapod crustacean predator on small crustaceans, polychaetes, and

Table 3 Comparison of estimated standing crops (in numbers and biomass) of pink shrimp and blue crab among selected habitat types in spring (May–June) and fall (September) 2006

Habitat type	Area (ha)	Pink shrimp standing crop				Blue crab standing crop			
		Spring 2006		Fall 2006		Spring 2006		Fall 2006	
		Number	Biomass (g)	Number	Biomass (g)	Number	Biomass (g)	Number	Biomass (g)
<i>Spartina</i> edge	0.3	930	6	12,741	866	620	1,721	9,304	112
<i>Juncus</i> edge	1.1	3,536	21	25,913	1,699	23,598	101,665	18,882	5,151
Seagrass	148.2	8,722,003	1,093,399	26,174,897	1,506,757	3,620,957	174,825	3,346,867	254,830
SNB	166.2	2,392,907	14,956	6,646,964	33,235	2,215,101	149,557	737,813	29,911

Standing crops were estimated by combining density and biomass data from nekton samples and the areal coverage of each habitat type estimated from aerial photography

Fig. 3 Regression tree showing the distribution of juvenile pink shrimp in May–June 2006. Each split in the tree includes the name of the explanatory variable, number of cases (N), mean density (number per square meter), and the standard deviation (SD). The cumulative and cross-validated R^2 values for the whole model are 0.255 and 0.203, respectively



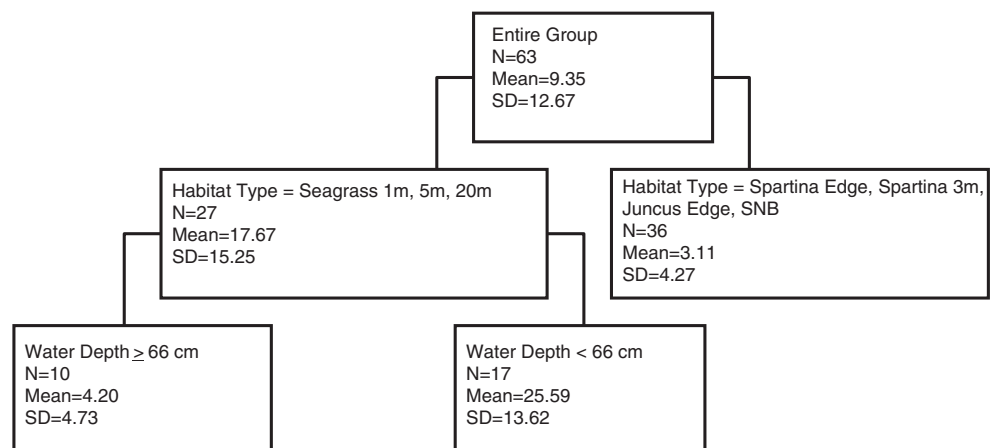
mollusks in seagrass beds (Nelson 1981; Livingston 1984; Leber 1985; Corona et al. 2000). The estuarine resident species, daggerblade grass shrimp and rainwater killifish, also had higher densities at seagrass sites than at the marsh edge. This pattern is clearly different from the distribution of penaeid shrimps and other species reported from estuaries in the north-central and northwestern GoM where seagrass or other species of submerged aquatic vegetation (SAV) are absent; at these locations, high nekton densities are concentrated at the marsh edge (Baltz et al. 1993; Minello et al. 1994; Peterson and Turner 1994; Minello 1999; Rozas and Zimmerman 2000).

Nekton assemblages at nearshore seagrass or SAV sites often include taxa more commonly associated with flooded marsh vegetation, and the densities of these species decline with distance away from the marsh shoreline (Raposa and Oviatt 2000; Rozas and Minello 2006). This distribution pattern, however, was not apparent in our study. A significant location effect within the seagrass was detected in our study for only two species, which showed opposite patterns of distribution. Darter goby fit the pattern reported from previous studies and was more abundant at nearshore (seagrass 1 m) sites than at seagrass sites 20 m from shore. Marsh grass shrimp (spring), blue crab (fall), and rainwater killifish (fall) also generally decreased with distance from shore, but no significant location effect was detected for these species in our analysis. In contrast, pink shrimp was

more abundant in seagrass located 20 than 1 m from shore. Within seagrass beds of a New England estuary, several species, including rainwater killifish and daggerblade grass shrimp, are more abundant at sites located near (3 and 10 m) the marsh shoreline than at sites farther (150 and 300 m) away (Raposa and Oviatt 2000). Perhaps the three distances we used in our study design were not sufficient (all too near the marsh) to resolve this pattern.

Although numerous studies have compared nekton abundance in seagrass and other estuarine habitat types, marsh has seldom been included in these comparisons (Irlandi and Crawford 1997; Heck et al. 2003). In a south Texas estuary where SAV (mixed *H. wrightii* and *Ruppia maritima*) and salt marsh co-occur, nekton densities in SAV and *Spartina* edge are not significantly different for most species, but significantly higher at marsh edge sites for blue crab, daggerblade grass shrimp, and brackish grass shrimp and higher in SAV for brown shrimp in spring (Rozas and Minello 1998). Most studies of seagrass- and SAV-dominated systems, however, show that nekton is either more abundant in seagrass/SAV beds than marsh vegetation or evenly distributed between these two habitat types. Blue crab in Christmas Bay (upper Texas coast) is more abundant in *H. wrightii* than *Spartina* marsh edge (Thomas et al. 1990) and is more abundant in seagrass beds than *Spartina* marshes of lower Mobile Bay, Alabama (Heck et al. 2001). Densities of pink shrimp and brown shrimp in

Fig. 4 Regression tree showing the distribution of juvenile pink shrimp in September 2006. Each split in the tree includes the name of the explanatory variable, number of cases (N), mean density (number per square meter), and the standard deviation (SD). The cumulative and cross-validated R^2 values for the whole model are 0.618 and 0.569, respectively



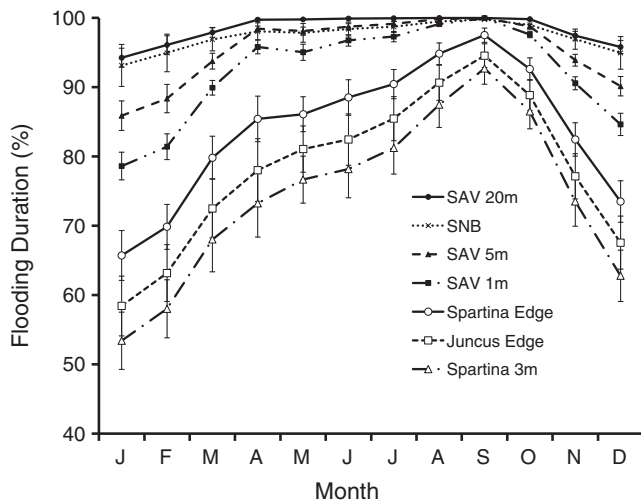


Fig. 5 Average monthly flooding durations [(hours sites inundated/total hours in month) \times 100] of habitat types within the study area. Error bars, 1 SE. Means and SEs were calculated from 18 samples taken in each habitat type

Mobile Bay are higher in *R. maritima* beds than *Spartina* marsh (Howe and Wallace 2000). Nekton abundance and species richness are higher in seagrass or macroalgae than at marsh sites in a New England estuary (Meng et al. 2004). Comparisons of nekton densities between emergent marsh and SAV in tidal freshwater and oligohaline systems reveal similar patterns (Castellanos and Rozas 2001; Rozas and Minello 2006, 2010).

The nekton distribution patterns we observed within *Spartina* marsh were not consistent with the results of previous studies conducted in the north-central and north-western GoM that show a sharp decline in densities of penaeid shrimps and blue crab with distance from shore (Peterson and Turner 1994; Minello 1999; Minello et al. 2008). Our analysis detected no significant difference in the densities of pink shrimp or blue crab within *Spartina* marsh between sites 3 m from shore and sites at the marsh edge. Penaeid shrimp densities within the marsh in our study area were relatively low and may have been too variable to detect a pattern. Only two species in our study, brackish grass shrimp and darter goby, showed a significant decline in abundance with distance into the marsh. Daggerblade grass shrimp (spring) showed the opposite pattern.

Vegetation structure is generally beneficial, but natant organisms may avoid vegetation with high structural complexity if it interferes with movement or foraging activity. *Juncus* marsh, which occupied most (79%) of the shoreline in our study area, was structurally more complex (four to six times higher stem density) than *Spartina* marsh edge, and we anticipated that this high structural complexity would reduce nekton use of *Juncus* marsh. This was not the case, however, and nekton densities were either similar or higher (e.g., pinfish in fall) in *Juncus* compared with

Spartina marsh. Although pink shrimp densities were relatively low within the *Juncus* marsh, the mean density we observed in fall (2.4 ± 0.60) is not inconsequential considering the total area of available *Juncus* shoreline habitat in the system. Previous comparisons of *Juncus* and *Spartina* marsh in Texas bays are conflicting, with Zimmerman et al. (1990) showing similar use by nekton in Lavaca Bay and Rozas and Zimmerman (2000) reporting lower nekton densities in *Juncus* from East Galveston Bay. These reduced densities in East Galveston Bay, however, may have been related to flooding patterns rather than stem density. The flooding duration in our study was similar for *Spartina* and *Juncus* marsh edge (annual mean, 84% vs. 78%), whereas in East Galveston Bay, annual flooding of *Juncus* (34%) was substantially lower than for *Spartina* (66%).

We collected few species or individuals at open water sites where seagrass was absent. Even though the use of *Spartina* edge sites was relatively low, species richness (spring) and the densities of several taxa were higher at these marsh sites than over SNB. This pattern of greater use of vegetated sites than SNB is consistent with numerous previous studies (e.g., Briggs and O'Connor 1971; Orth et al. 1984; Lubbers et al. 1990; Williams et al. 1990; Sogard and Able 1991; Connolly 1994; West and King 1996; Minello 1999; Minello et al. 2003; Heck et al. 2003).

Overall, water quality appeared high in the study area, and environmental conditions were similar among habitat types. Environmental characteristics that separated habitat types most were related to site elevation (water depth) and structural complexity. The high (>90%) flooding duration of seagrass sites provided an almost continuous accessibility for aquatic organisms. Although marsh sites were flooded for shorter periods, and therefore were less available to nekton than seagrass sites, the flooding patterns we observed in our study area would not explain the differences in marsh use by penaeid shrimps between our study area and other locations in the northwestern GoM. The flooding duration for *Spartina* edge in our study area (annual mean=84%) was at least as high as that reported for three locations in Texas where the use of *Spartina* marsh by penaeid shrimps is relatively high: Galveston Bay=78% (Minello and Webb 1997) and 82–100% (Whaley 1997); East Galveston Bay=66% (Rozas and Zimmerman 2000); and Carlos Bay, Mesquite Bay, and Ayres Bay=72% (Rozas and Minello 1998).

Estuarine residents and the young of fishery species in this lagoonal system were mainly supported by seagrass habitat and, to a lesser extent, by salt marsh. Although the densities for some nekton species were similar when both habitat types were flooded, our conclusion regarding the relative importance of seagrass in this system was based on the significantly lower densities in marsh for some species,

a lower areal extent of marsh edge, and the relatively low flooding duration of marsh. Nekton was not concentrated at the marsh edge as in the salt marsh-dominated systems of the north-central and northwestern GoM. In particular, the densities and standing crop estimates of juvenile pink shrimp were highest in seagrass, corroborating much previous work recognizing seagrass beds as an important nursery habitat for this species. In contrast to other studies (Raposa and Oviatt 2000; Minello and Rozas 2002; Rozas and Minello 2006), our results did not reveal any significant location effects within seagrass or *Spartina* marsh.

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Appendix 1

Table 4 Comparison of biomasses, mean per square meter and (SE), in grams of dominant (contributing most biomass) decapod crustaceans and fishes collected among seven habitat types including *Spartina* edge and *Juncus* edge ≤ 1 m from shore; *Spartina* 3 m from shore; seagrass 1, 5, and 20 m from shore; and SNB in May–June and September 2006

Species	<i>Spartina</i> 3 m		<i>Spartina</i> edge		<i>Juncus</i> edge		Seagrass 1 m		Seagrass 5 m		Seagrass 20 m		SNB		Total number collected	Habitat effect <i>p</i> value	Contrast <i>p</i> values					
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	(1) <i>Spartina</i> edge vs. seagrass	(2) <i>Spartina</i> edge vs. <i>Spartina</i> SNB			(3) <i>Spartina</i> edge vs. <i>Spartina</i> 3 m	(4) <i>Spartina</i> edge vs. <i>Juncus</i> edge	(5) Seagrass 1 m vs. 5 m	(6) Seagrass 1 m vs. 20 m		
May–June 2006																						
Crustaceans	11.5	(5.81)	7.6	(4.48)	13.4	(6.47)	3.4	(1.85)	10.6	(6.72)	6.7	(3.24)	0.3	(0.21)	522.9	0.1132						
Blue crab	0.6	(0.60)	0.6	(0.56)	9.6	(6.48)	0.1	(0.04)	0.2	(0.12)	0.1	(0.04)	0.1	(0.08)	100.9	0.2326						
Thinstripe hermit crab	1.7	(0.83)	3.6	(2.09)	1.7	(0.89)	1.4	(1.06)	0.3	(0.19)	0.1	(0.08)	0.0	(0.01)	79.5	0.1385						
Atlantic mud crab	0.0	(0.00)	3.1	(3.06)	0.6	(0.61)	0.4	(0.38)	2.5	(2.18)	0.0	(0.00)	0.0	(0.00)	59.3	0.5180						
Fishes	11.9	(8.29)	5.1	(1.96)	7.5	(3.06)	4.7	(1.92)	2.9	(1.71)	9.5	(3.34)	1.0	(0.71)	383.1	0.1125						
Pinfish	10.3	(8.36)	1.1	(0.45)	3.6	(1.99)	2.6	(1.16)	1.7	(1.17)	8.2	(3.29)	0.3	(0.29)	250.8	0.0745						
Spot	0.1	(0.09)	2.2	(1.35)	1.4	(0.94)	0.2	(0.15)	0.0	(0.00)	0.7	(0.65)	0.6	(0.63)	46.3	0.1872						
September 2006																						
Crustaceans	1.4	(0.72)	2.8	(1.37)	5.7	(1.27)	4.4	(1.67)	5.1	(2.21)	4.7	(1.88)	3.4	(2.89)	294.0	0.1493						
Bigelow snapping shrimp	0.0	(0.00)	0.3	(0.20)	1.2	(0.53)	3.2	(1.14)	3.1	(1.52)	2.6	(1.30)	0.3	(0.31)	96.5	0.0119	0.0102	0.9570	0.6161	0.2155	0.5600	0.2811
Pink shrimp	0.1	(0.05)	0.3	(0.21)	0.2	(0.12)	0.6	(0.36)	0.9	(0.35)	1.6	(0.63)	0.0	(0.01)	32.5	0.0074	0.0530	0.3733	0.5318	0.7127	0.3208	0.0505
Brackish grass shrimp	0.1	(0.07)	1.2	(0.87)	0.5	(0.09)	0.2	(0.21)	0.5	(0.22)	0.2	(0.11)	0.0	(0.00)	24.3	0.0474	0.0466	0.0051	0.0119	0.5288	0.3020	0.9156
Thinstripe hermit crab	0.4	(0.22)	0.1	(0.08)	1.9	(0.84)	0.0	(0.03)	0.0	(0.01)	0.0	(0.03)	0.7	(0.48)	28.2	0.0034 ^a	0.7799	0.2541	0.4375	0.0009	0.9451	0.9671
Atlantic mud crab	0.0	(0.00)	0.0	(0.00)	1.2	(1.15)	0.0	(0.00)	0.0	(0.00)	0.3	(0.32)	1.5	(1.47)	26.7	0.6347						
Fishes	1.9	(0.59)	6.6	(2.87)	50.3	(26.32)	5.8	(1.86)	10.1	(4.59)	20.2	(13.63)	11.6	(11.23)	958.4	0.0057	0.6742	0.2253	0.3538	0.0070	0.5736	0.8896
Pinfish	0.2	(0.21)	1.4	(1.20)	10.2	(4.81)	2.9	(1.06)	4.0	(1.74)	16.0	(11.04)	0.0	(0.00)	311.9	0.0072	0.0810	0.4478	0.5973	0.0091	0.8809	0.5365
American eel	0.0	(0.00)	0.0	(0.00)	26.4	(26.40)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	237.6	0.4346						
White mullet	0.0	(0.00)	2.1	(2.13)	8.5	(6.16)	0.0	(0.00)	3.2	(3.19)	0.0	(0.00)	10.9	(10.92)	222.7	0.5503						
Rainwater killifish	0.4	(0.12)	1.2	(0.72)	0.8	(0.34)	0.4	(0.19)	1.0	(0.47)	0.0	(0.04)	0.0	(0.00)	33.9	0.0327	0.1277	0.0104	0.3057	0.6952	0.1378	0.2980

Each mean is estimated from nine samples. The results (*p* values) are given for ANOVA analyses used to compare all habitat types (habitat effect) and six a priori contrasts testing different habitat combinations

^a The ANOVA probability value was significant at the 5% level after alpha was adjusted as described by Rice (1989). Contrast *p* values were not adjusted

Appendix 2

Table 5 Comparison of environmental characteristics among habitat types

Variable	<i>Spartina</i> 3 m			<i>Spartina</i> edge			<i>Juncus</i> edge			Seagrass 1 m			Seagrass 5 m			Seagrass 20 m			SNB		Habitat effect <i>p</i> value	Contrast <i>p</i> values					
	Mean	SE		Mean	SE		Mean	SE		Mean	SE		Mean	SE		Mean	SE		Mean	SE		(1) <i>Spartina</i> edge vs. seagrass	(2) <i>Spartina</i> edge vs. SNB	(3) <i>Spartina</i> edge vs. <i>Spartina</i> 3 m	(4) <i>Spartina</i> edge vs. <i>Juncus</i> edge	(5) Seagrass 1 m vs. 5 m	(6) Seagrass 1 m vs. 20 m
May–June 2006																											
Water temperature (°C)	29.2	(0.98)	30.1	(0.68)	30.5	(0.44)	30.3	(0.82)	30.3	(0.49)	30.5	(0.49)	30.5	(0.49)	30.9	(0.42)	0.6791										
Salinity	35.3	(0.41)	35.6	(0.24)	35.2	(0.22)	34.9	(0.26)	35.2	(0.28)	34.9	(0.31)	34.8	(0.15)	0.4082												
Water depth (cm)	32.4	(2.97)	39.6	(3.57)	35.0	(4.23)	42.2	(3.07)	52.4	(4.91)	68.6	(7.43)	83.3	(9.36)	0.0001 ^a						0.0241	0.0001	0.3660	0.5622	0.1983	0.0014	
Dissolved oxygen (mg l ⁻¹)	4.9	(0.52)	5.2	(0.58)	5.6	(0.53)	5.9	(0.72)	6.6	(0.59)	6.7	(0.64)	6.8	(0.42)	0.1483												
Turbidity (FTU)	0.3	(0.15)	0.3	(0.07)	0.3	(0.16)	0.7	(0.19)	0.7	(0.22)	0.7	(0.23)	0.7	(0.21)	0.2615												
Distance to marsh edge (m)	3.1	(0.09)	0.8	(0.16)	0.8	(0.14)	1.4	(0.37)	4.3	(0.31)	18.9	(0.58)	104.8	(34.81)	0.0001 ^a						0.6283	0.0001	0.9049	0.9995	0.8749	0.3499	
Distance to SAV edge (m)	1.8	(0.97)	1.4	(0.76)	0.8	(0.17)	2.3	(0.57)	16.5	(0.98)	5.8	(1.90)	0.0001 ^a							0.0001	0.0045	0.2501	0.7384	0.2739	0.0001		
SAV cover (%)	249.7	(68.61)	141.4	(50.79)	538.8	(82.08)	88.9%	(7.3%)	94.4%	(5.6%)	91.1%	(8.9%)	0.8674							0.0929	0.0001						
Stem density (stems per square meter)															0.0001 ^a												
September 2006																											
Water Temperature (°C)	27.2	(0.39)	28.4	(0.33)	27.8	(0.51)	28.0	(0.67)	27.9	(0.56)	28.1	(0.46)	28.0	(0.44)	0.7480												
Salinity	28.6	(1.18)	28.4	(0.56)	28.2	(0.89)	30.0	(0.58)	28.7	(0.96)	30.1	(0.59)	29.9	(0.75)	0.4131												
Water depth (cm)	36.3	(4.13)	39.7	(5.73)	31.5	(3.58)	50.3	(5.44)	60.4	(7.42)	72.3	(7.25)	67.7	(6.47)	0.0001 ^a						0.0027	0.0014	0.6861	0.3295	0.2310	0.0105	
Dissolved oxygen (mg l ⁻¹)	4.4	(0.56)	6.3	(1.21)	4.5	(0.66)	4.6	(1.12)	5.2	(1.07)	5.2	(0.75)	6.1	(0.81)	0.6475												
Turbidity (FTU)	8.4	(1.95)	29.9	(22.07)	21.3	(6.55)	4.1	(0.71)	2.5	(0.43)	3.0	(0.43)	2.3	(0.26)	0.1683												
Distance to marsh edge (m)	3.0	(0.14)	0.9	(0.08)	1.0	(0.07)	1.6	(0.13)	4.9	(0.35)	19.3	(0.97)	49.7	(18.64)	0.0001 ^a						0.3464	0.0001	0.8341	0.9912	0.7413	0.0816	
Distance to SAV edge (m)	2.8	(0.98)	2.3	(0.34)	1.1	(0.18)	3.1	(0.59)	15.2	(2.35)	12.2	(7.76)	0.0037 ^a							0.3093	0.0365			0.9015	0.6389	0.0020	
SAV cover (%)	183.9	(55.15)	74.4	(28.67)	440.6	(65.32)	93.3%	(5.5%)	100%	(0.0%)	98.9%	(1.1%)	0.3175							0.0270	0.0001 ^a						
Stem density (stems per square meter)															0.0001 ^a												

Mean and (SE) are given for variables measured in each habitat type that we sampled in May–June and September 2006. Each mean was estimated from nine samples. The results (*p* values) are given for ANOVA analyses used to compare all habitat types (habitat effect) and six a priori contrasts testing different habitat combinations

^aThe ANOVA probability value was significant at the 5% level after alpha was adjusted as described by Rice (1989). Contrast *p* values were not adjusted

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